

Functional Morphology of the Lemuriform Wrist Joints and the Relationship Between Wrist Morphology and Positional Behavior in Arboreal Primates

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ABSTRACT A comparative study of carpal joint structure and function in six Malagasy lemuriforms was undertaken to test predicted morphoclines in carpal joint morphology between pronograde and orthograde arboreal primates. Patterns of movement at the wrist during locomotion were observed and described for the lemuriform species *Lemur fulvus* and *Propithecus verreauxi*. *Lemur fulvus*, which assumes a pronograde posture during locomotion, extends and pronates the wrist during the support phase of quadrupedal walking and running stride cycles. Furthermore, the forearm of this species exhibits some transverse movement across the proximal wrist joint during the support phase. In contrast, the indriid *Propithecus* maintains the hand and wrist in a flexed and partially supinated position during vertical clinging and suspensory postures.

Habitual quadrupedal and vertical postures in Malagasy primates are in turn related to very different patterns of carpal joint morphology and articular mechanics. Those lemurs which are predominantly pronograde share a series of structural features related to stabilizing the antebrachiocarpal joint during extension and mediolateral deviation and the midcarpal joint during pronation: an intraarticular labrum is present on the inner portion of the radiocarpal ligament, the radiocarpal articular surface is quite flat dorsoventrally, the capitate-trapezoid embrasure is expanded dorsally, and development of the radial and ulnar styloids is more pronounced. The wrists of *Propithecus*, *Avahi*, and *Lepilemur* (vertical clingers) differ from those of quadrupedal lemuriforms in possessing a suite of morphological features related to stabilizing the wrist during antebrachiocarpal flexion and midcarpal supination: the radiocarpal articular surface is deeply curved and tilted anteriorly, the dorsal radiocarpal ligament is very broad, thick, and fibrous, the hamate's triquetral facet is directed proximodistally, and the capitate-trapezoid embrasure is dorsally constricted and expanded palmarly. These observed contrasts in carpal form and function are used to define further the morphological features related to orthograde posture in several lineages of arboreal primates. © 1996 Wiley-Liss, Inc.

The wrist joints of arboreal mammals are extremely complex in both their morphology and function. Positional behaviors on irregular, discontinuous, arboreal supports require compromises between wrist joint mobility and stability which place a wide range of mechanical demands on carpal joint morphology (Yalden, 1972). Primates are more diverse in their positional behaviors than

perhaps any other order of placental mammals (Simons, 1972; Fleagle, 1988), and not surprisingly the anatomy of the wrist is exceptionally variable within the Order Pri-

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mates (Martin, 1990). As such, study of primate carpal joint structure and analyses of carpal function provide morphologists the opportunity to relate this structural variation to functional differentiation.

The studies of Lewis (1965, 1969, 1971, 1972) generated tremendous interest in the functional relationship between primate wrist joint morphology and positional behavior by relating several morphological specializations of the hominoid wrist to a specific mode of arboreal locomotion. The derived features of the hominoid wrist which Lewis (1965, 1969) identified included a reduced ulnar styloid separated from the carpus by a soft tissue meniscus, a fully diarthrodial inferior radioulnar joint, and a pisiform which no longer articulates with the ulna. Lewis believed these morphological novelties enabled hominoids to rotate the wrist extensively and, furthermore, that wrist rotation was a necessary prerequisite for bimanual suspensory locomotion. Lewis concluded the common ancestor of hominoids must have also possessed these morphological features, and therefore must have also practiced some form of 'brachiation.'

Subsequent authors presented evidence which drew into question the biological role(s) associated with the functional complexes identified by Lewis (1971, 1972). Cartmill and Milton (1974, 1977) demonstrated that ulnocarpal and inferior radioulnar joint morphologies similar to those observed in the hominoid wrist are also found in the wrist joints of lorissine primates—prosimians which practice a slow-climbing form of arboreal locomotion. Mendel (1979) also showed that morphological specializations of the wrist joints analogous to those of hominoids are found in two-toed sloths. Mendel's (1979) results lent additional support to Cartmill and Milton's (1977) contention that the derived features of the hominoid wrist may in fact be related to slow, deliberate, quadrumanous climbing. Sarmiento (1987, 1988) has argued that those features of the hominoid wrist specifically related to enhanced rotation could also be viewed as structural adaptations for forelimb supination during vertical climbing.

Despite considerable debate surrounding the positional behaviors inferred for early

hominoids, most authors would agree that wrist morphology of quadrupedal monkeys is quite distinctive from that of the more orthograde apes. However, contrasts in wrist morphology between living pronograde and orthograde primates have not extended far beyond these hominoid, non-hominoid comparisons. This is surprising given the fact that habitual vertical postures, in the form of either vertical clinging, vertical climbing, or below-branch suspension, have been argued at one time or another to have characterized the earliest primates (Napier, 1967; Napier and Walker, 1967; Beard, 1991), ancestral lemurs (= lemurid + indriid clade; Gebo, 1985; Gebo and Dagosto, 1988), ancestral hominoids (Sarmiento, 1987), or the ancestors of bipedal hominids (Fleagle et al., 1981). Identification of additional form-function complexes related to specific orthograde postural and locomotor behaviors in extant arboreal primates are needed to further investigate patterns of primate postural evolution.

The Malagasy lemuriforms are diverse in many aspects of their biology including positional behavior, which ranges from vertical clinging and leaping to arboreal and terrestrial quadrupedalism (Tattersall, 1982). The aim of this study was to test predicted morphoclines in carpal joint morphology between pronograde and orthograde lemuriforms, in order to clarify further the morphological features associated with pronograde and orthograde positional behaviors in arboreal primates. The evolutionary significance of these findings is discussed with reference to the origin of orthograde posture in several extant primate clades and in the early Tertiary primate genera *Notharctus* and *Smilodectes*.

HYPOTHESES

Earlier studies of primate carpal form and function have established morphoclines in wrist joint morphology between primates which are essentially pronograde and those which frequently use more orthograde postures. These morphoclines permit several predictions to be made *a priori* regarding expected patterns of carpal morphology in lemuriforms which are either active arboreal

quadrupeds (AAQs) or vertical clingers (VCs).¹ The inferior radioulnar joint of pronograde arboreal primates such as *Cebus* and *Procolobus* is a very stable syndesmosis and the ulnar head is relatively small, which allows very little movement of the radius about the ulna (Lewis, 1974). In contrast, the ulnar head is globular and the joint is partially or fully diarthrodial in lorises and hominoids, thus enabling the radius to rotate freely about the ulna (Lewis, 1972, 1974; Cartmill and Milton, 1977). Quadrupedal lemuriforms (AAQs) are therefore predicted to bear a relatively small ulnar head and syndesmotomic inferior radioulnar joint whereas VCs should possess a more mobile inferior radioulnar joint (e.g. synovial joint, large ulnar head).

The ulnocarpal and radiocarpal joints are weight-bearing joints in most pronograde primates. The radiocarpal joints of these pronograde forms are relatively flat to resist unidirectional weight-bearing loads, whereas those of more orthograde taxa are curved to remain stable throughout a wider range of joint movements (Sarmiento, 1988). Furthermore, pronograde primates have a mediolaterally wide radiocarpal articulation and robust radial and ulnar styloids which stabilize the antebrachicarpal joint against transverse displacements during weight-bearing postures (Tuttle, 1967; O'Connor, 1975; Fleagle and Meldrum, 1988; Sarmiento, 1988). In contrast, orthograde primates do not possess such an expanded radiocarpal articulation, and taxa such as lorises and hominoids possess a reduced ulnar styloid (Lewis, 1969, 1989; Cartmill and Milton, 1977). Lemuriform AAQs are thus predicted to have 1) relatively flatter radiocarpal conarticular surfaces, 2) a mediolaterally expanded radiocarpal articulation, and 3) relatively longer radial and ulnar styloids.

The midcarpal joints of quadrupedal primates must bear compressive forces from the forelimb, and these taxa have a proximally facing triquetrohamate facet to support

weight-bearing loads transmitted from the forelimb to the carpus (Jenkins and Fleagle, 1975; Fleagle, 1977; Sarmiento, 1988). The proximally directed triquetrohamate facet of these quadrupeds gives the convex midcarpal joint surface a somewhat flat shape in dorsal view. The midcarpal joints of more orthograde primates are not frequently subjected to such loading patterns, and these taxa have a tightly curved midcarpal surface with a more distally directed triquetrohamate facet (Jenkins and Fleagle, 1975; Fleagle, 1977; Fleagle and Meldrum, 1988; Sarmiento, 1988). Lemuriform AAQs are thus predicted to have a relatively flat midcarpal surface whereas VCs are expected to possess a more tightly curved midcarpal surface.

Finally, primates which frequently climb and cling on vertical arboreal supports use a powerful thumb to grasp the substrate (Van Horn, 1972; Cartmill, 1974). Lemuriform VCs possess a thumb which is separated from the other digits by an interdigital cleft, which allows the hand to securely clasp large vertical supports between the thumb and postaxial rays (Cartmill, 1974). Vertical clinging likely requires prolonged contraction of the thenar muscles to maintain a secure grasp, which produces considerable transarticular forces across the pollical carpometacarpal articulation. Lemuriform VCs are expected to have an expanded carpometacarpal articular surface compared to AAQs in order to increase the bearing area, and therefore reduce joint stress, at the pollical carpometacarpal joint.

MATERIALS AND METHODS

Positional behavior

Descriptions of lemuriform locomotor and postural behaviors are available in Walker (1979), Tattersall (1982), Gebo (1987), Oxnard et al. (1990), and Dagosto (1994). Support preferences described for the species included in this study² are shown in Table 1

¹For the purpose of discussion, lemuriforms included in this study which are active arboreal quadrupeds are abbreviated as AAQ whereas those which are habitual vertical clingers are abbreviated as VC (locomotor classification after Walker, 1974).

²Nomenclature follows Tattersall and Schwartz (1991). Groves and Eaglen (1988), Simons and Rumpler (1988), and Yoder (1994) have argued that the generic designation for *Lemur catta* be changed to *Eulemur* to recognize a *L. catta*-*Hapalemur* clade. All AAQs in this study are assigned to the genus *Lemur*, following Tattersall and Schwartz (1991), for ease of communication and discussion.

TABLE 1. Support preferences and sample sizes for lemuriform species included for kinematic analysis, dissection, and osteological measurements

Species	Support orientation	Kinematic ^d	Cadaver	Skeletal
Arboreal quadrupeds (AAQs)				
<i>Lemur fulvus</i>	horizontal (69.3%) ^a oblique (26.8%)	2 (103)	2	16
<i>Lemur variegatus</i>	horizontal (58.1%) ^a oblique (41.5%)	—	2	18
<i>Lemur catta</i>	horizontal, oblique ^{b,c}	—	1	20
Vertical clingers (VCs)				
<i>Propithecus verreauxi</i>	vertical ^c	4 (31)	1	18
<i>Avahi laniger</i>	vertical ^c	—	3	11
<i>Lepilemur mustelinus</i>	vertical ^c	—	3	18
Total		6 (134)	12	101

^a Dagosto, 1994.^b Walker, 1979.^c Oxnard et al., 1990.^d Number of individuals (number of bouts) observed.

and frequencies are given where known. Unfortunately these sources do not provide suitably detailed descriptions of hand and forelimb use during locomotion in these primates. In order to further investigate wrist postures characteristic of pronograde and orthograde lemuriforms, postures of the hand and forelimb during locomotion were examined in captive individuals of *Lemur fulvus* and *Propithecus verreauxi* (Table 1). These observations were recorded in a seminatural environment at the Duke University Primate Center, Durham, North Carolina.

Locomotor bouts were filmed in either frontal or lateral view at 60 fields per second with a high speed shutter setting (1/250 sec) using a standard videorecorder. Film sequences of animals moving strictly parallel (frontal view) or perpendicular (lateral view) to the plane of the camera were analyzed qualitatively from extensively edited videotape using a Panasonic video subsystem (Panasonic 6300ag videorecorder, Panasonic CT1400mg RGB monitor, Peak Performance 2D Motion Analysis software) equipped with stop-action and single-frame advance playback. Qualitative observations such as positions of the palm, pollex, and digits II–V, instances of extension and flexion at the antibrachiocarpal joint, and instances of radial and ulnar deviation at the antibrachiocarpal joint were noted for each sequence. *L. fulvus* locomotor sequences included for analysis include initial touchdown, mid-stance, and lift-off of the support phase dur-

ing quadrupedal stride cycles. Sequences observed for *Propithecus* include vertical clinging, resting and feeding postures, and occasional antipronograde behaviors.

Osteoligamentous morphology

Cadaver specimens representing three species of VCs (Table 1) and three species of AAQs (Table 1) were dissected with the aid of a light microscope. Following removal of the hand musculature, osteoligamentous preparations were manipulated to examine potential movements at the carpal joints. The capsular apparatus and intercarpal ligaments were then described and illustrated. The ligaments function as tensile members of the carpal complex during climbing and suspension, and from a mechanical standpoint are as important as the compressive members (bones) for understanding the structural integrity of the carpal system (Jouffroy, unpub.). The ligaments also function as 'brakes' which limit the potential range of joint motion (MacConnail, 1973). Description of the intercarpal ligaments thus contributes mechanically relevant information not discernible from a study of bony anatomy alone, and provides an additional test of predicted structural and functional patterns. Radiographs of several cadaver specimens were taken prior to dissection to observe the spatial and structural interrelationships of the carpal bones to one another with the musculoskeletal system intact.

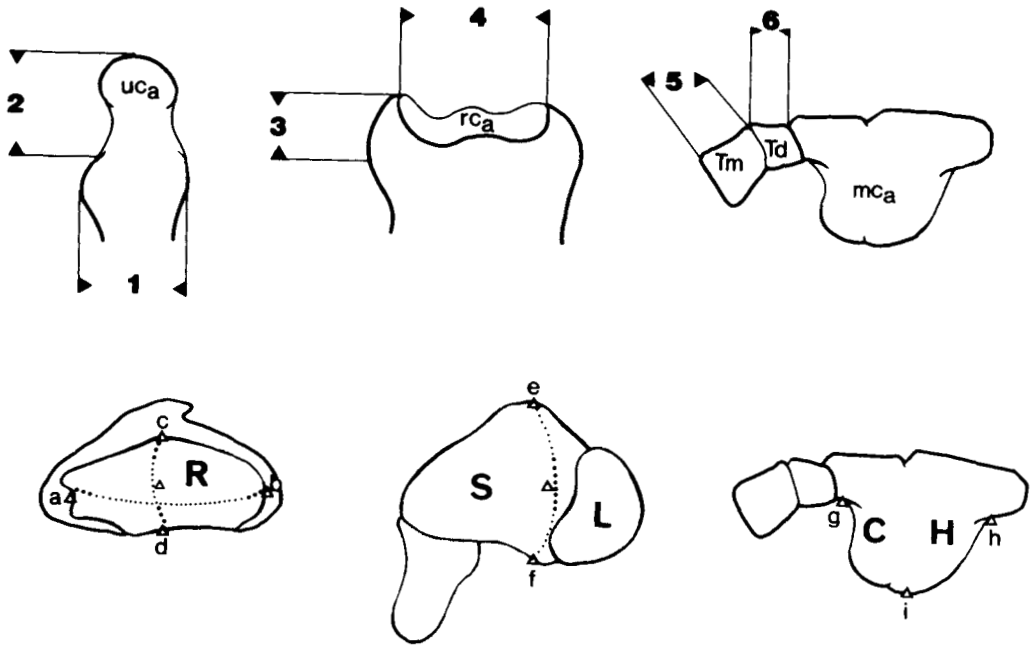


Fig. 1. Measurements referred to in this study. Linear measurements (**top row**) are: 1, ulnar head breadth; 2, ulnar styloid length; 3, radial styloid length; 4, radiocarpal articular breadth; 5, trapezium breadth; and 6, trapezoid breadth. Measurements are defined as follows: 1, maximum mediolateral breadth of the ulnar head; 2, proximodistal length from the most distal point on the ulnar head to the distal tip of the ulnar styloid; 3, proximodistal length from the distal radial diaphyseal-epiphyseal suture to the distal tip of the radial styloid; 4, maximum mediolateral breadth of the radiocarpal articular surface; 5, maximum mediolateral breadth of the trapezium's carpometacarpal articular surface; 6, maximum mediolateral breadth of the trapezoid's carpometacarpal articular surface. Arc lengths and curva-

tures (**bottom row**) are: a-b, mediolateral radiocarpal curvature and arc length; c-d, dorsoventral radiocarpal curvature and arc length; e-f, dorsoventral scaphoid curvature and arc length; and g-i-h, mediolateral midcarpal curvature and arc length. The small triangles represent points which were digitized on the bones to obtain curvature measurements. Abbreviations: uc, ulnocarpal facet; rc, radiocarpal facet; mc, midcarpal articular surface; Tm, trapezium; Td, trapezoid; R, radius; S, scaphoid; L, lunate; C, capitate; and H, hamate. The small dots on the articular surface of the radius (R) and scaphoid (S) do not represent actual digitized points but are used for schematic purposes to illustrate the contours which were digitized to obtain arc lengths.

Osteometrics

In order to test predicted morphoclines in bony carpal morphology between pronograde and orthograde lemuriforms, a large sample of skeletal specimens (Table 1) representing six species of Malagasy lemuriforms were measured for linear and three dimensional morphometric analysis. Linear metrics (Fig. 1) were taken using dial calipers. Previous attempts to quantify morphological variation of the carpal joints utilized only linear measures of joint surfaces to capture shape variation (Corruccini et al., 1975; Corruccini, 1977; Etter, 1978). However, linear dimensions of synovial articular units can

bear little overall relation to those parameters which actually affect joint stability and angular displacement—namely the curvature and arc length of the conarticular surfaces. Curvatures and arc lengths of wrist joint articular surfaces were measured in this study using a COMP 3D High Precision Reflex Microscope (MacLarnon, 1989). Arc lengths were calculated at the proximal and midcarpal joints (Fig. 1) by digitizing ten points along the articular arc and then computing the sum of the linear distances between the digitized points. Curvature of the articular arc was measured as the included angle subtending the arc of the articular sur-

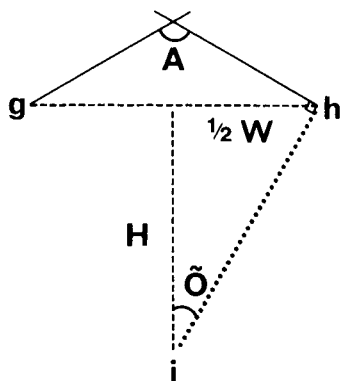


Fig. 2. Diagram showing parameters used to calculate the curvature of joint surfaces. Three digitized points on the midcarpal articular surface (g, h, i; see Fig. 1) are shown. The included angle (A) varies according to the height (H) and chord length (W) of the articular arc. See text for details.

face. Replicability experiments demonstrate that arc lengths and dimensions used for calculating arc curvatures (see below) are repeatable between 3–5% error variance.

The subtended angle calculated here is not synonymous with that described by Susman et al. (1984) and Latimer and Lovejoy (1989). Specifically, the method used by these authors to calculate the subtended angle involves obtaining a radius of curvature by fitting the arc of a circle to the articular arc of the joint surface. The midcarpal joints of many specimens included in this study are much more similar in outline to a parabola than to the arc of a circle, and are so tightly curved in some cases that it is impossible to fit the arc of any circle to their outline. The included angle was calculated in this study by inscribing an isosceles triangle inside the articular arc and obtaining the angle between perpendiculars drawn normal to the sides of the triangle (Fig. 2). Linear dimensions used for calculating these joint curvatures were obtained by digitizing points at the beginning and end of the articular arc (e.g. points g and h in Figures 1, 2) and calculating the chord length between these points. The perpendicular distance from the chord to the articular arc (line H, Fig. 2) was then derived using Reflex software. The subtended angle (A) is an inferred angle

calculated from these two linear distances (Fig. 2) using the following formula:

$$\tilde{O} = \tan^{-1}[(.5*W)/(H)]$$

$$A = 2*(90 - \tilde{O}).$$

Extremely curved articular arcs have a low angle \tilde{O} and high included angle (A) whereas flatter surfaces have a more obtuse \tilde{O} and acute included angle (A). Calculated curvatures presented here include mediolateral and dorsoventral curvature of the distal radius radiocarpal facet, dorsoventral curvature of the scaphoid's radiocarpal facet, and mediolateral curvature of the convex midcarpal joint articular surface (Fig. 1). This method of measuring joint curvature is simply a means of expressing, quantitatively, the maximum height of the articular arc relative to its maximum chord length (Figs. 1, 2). This method does not capture more subtle variations in the articular arc contour.

Statistical analysis

Several statistical approaches were used to test predicted morphoclines in carpal joint shape between pronograde and orthograde lemuriforms. The linear carpal measurements included in this study were initially expressed as shape ratios. First, a new variable termed 'carpal size' was calculated for each individual. This new size variable is the geometric mean of 15 linear carpal dimensions. Each linear measurement shown in Figure 1 was then divided by this new size variable to derive new shape variables expressing shape of the radial and ulnar styloids, trapezoid, and trapezium in each individual. This procedure for creating shape variables follows that of Mosimann and James (1979) and Darroch and Mosimann (1985) except that the shape ratios used here were not logged for pairwise comparisons. Ratio and angular data are known to frequently violate the assumptions of parametric statistical tests (Sokal and Rohlf, 1981; Zar, 1984). Therefore, Kruskal-Wallis non-parametric tests were used to identify interspecific differences in these shape ratios and angular measurements and Kolmogorov-Smirnov tests used for pairwise species comparisons.

Possible allometric influences on the car-

TABLE 2. Summary statistics for linear measurements, joint articular arc lengths, and joint curvatures

Measurement*	Species					
	<i>Lepilemur</i>	<i>Propithecus</i>	<i>Avahi</i>	<i>L. variegatus</i>	<i>L. catta</i>	<i>L. fulvus</i>
Linear measurements						
1	3.25 (.44)	5.49 (.51)	3.85 (.32)	6.89 (.72)	5.24 (.66)	5.08 (.33)
2	2.45 (.33)	4.59 (.53)	3.12 (.42)	6.13 (.42)	3.98 (.62)	4.66 (.34)
3	1.58 (.26)	2.16 (.37)	1.44 (.55)	3.82 (.39)	2.62 (.40)	2.73 (.36)
4	5.32 (.62)	8.62 (.87)	6.15 (.31)	10.79 (.66)	7.13 (.87)	7.87 (.55)
5	3.15 (.48)	5.47 (.65)	3.73 (.59)	6.16 (.72)	4.05 (.43)	4.20 (.39)
6	1.89 (.31)	2.97 (.39)	2.08 (.23)	4.09 (.33)	3.18 (.39)	2.96 (.16)
Arc lengths						
a-b	5.13 (.58)	8.35 (.58)	6.09 (.33)	10.56 (.42)	6.73 (.45)	7.22 (.59)
c-d	2.53 (.38)	4.22 (.41)	3.24 (.31)	4.90 (.26)	3.49 (.31)	3.55 (.37)
e-f	3.93 (.88)	5.87 (.51)	4.52 (.71)	7.72 (.44)	5.05 (.81)	5.59 (.22)
g-h	7.45 (1.33)	14.27 (1.06)	9.68 (.81)	15.94 (1.01)	11.55 (1.3)	11.25 (.93)
Arc curvatures						
a-b	28.65 (5.43)	19.38 (6.77)	21.5 (5.74)	26.8 (4.33)	21.2 (6.85)	24.18 (9.1)
c-d	41.55 (9.93)	33.88 (10.63)	32.19 (4.19)	21.17 (5.64)	18.12 (5.61)	27.88 (7.31)
e-f	71.15 (6.81)	69.81 (5.04)	72.38 (12.4)	65.53 (5.25)	61.63 (6.86)	63.99 (11.14)
g-h	94.43 (7.66)	96.38 (5.47)	92.12 (4.67)	92.10 (5.48)	88.64 (6.3)	87.06 (8.48)

*Numbers and letters refer to measurements shown in Figure 1. Mean and (standard deviation) given for each species.

pal dimensions (Fig. 1) and shape ratios referred to in this study were first investigated by calculating Pearson correlation coefficients between these variables and two different size variables, carpal size and humeral midshaft diameter. Humeral midshaft diameter was chosen as a second size variable because it is strongly correlated ($r = .98$) with body mass in strepsirrhines, and scales very close to isometry (slope = .36; Demes and Jungers, 1993). The majority of linear measurements, angles, and ratios used here to quantify shape variation were all found to be significantly correlated with both estimated body size and overall carpal size ($P < .05$). Additional bivariate analyses were therefore necessary to test for between-group differences in carpal shape.

Analyses of covariance (ANCOVA) were used to test for differences between VCs and AAQs in the carpal dimensions shown in Figure 1. ANCOVA tests were performed between VCs and AAQs using the carpal dimensions shown in Figure 1 as dependent

variables and the two size measures as independent variables. ANCOVA tests were run only for those carpal variables found in regression analyses to show a significant relationship with the two size variables. Since some error is to be expected in these two size measures (Harvey and Pagel, 1991), both ordinary least squares (OLS) and reduced major-axis (RMA) slope and y-intercept values were calculated for all regressions in order to verify that both techniques produced similar results (Rayner, 1985). All regression and ANCOVA analyses were performed on log-transformed variables.

Finally, discriminant analysis was used to test for differences in carpal joint morphology between VCs and AAQs using the multivariate data set. A multivariate analysis of variance (MANOVA) was the preferred multivariate technique, since the primary objective is to test for differences between the centroids of groups which have been defined *a priori* (Neff and Marcus, 1980). Discriminant analysis of linear joint dimensions was

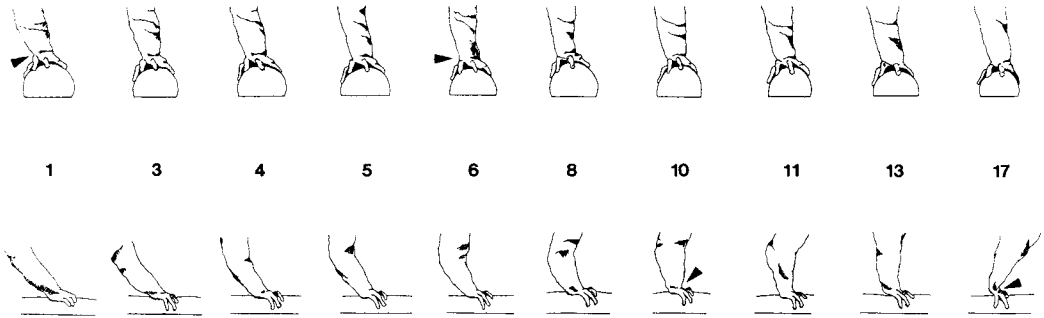


Fig. 3. Frontal (top) and lateral (bottom) views showing movements at the wrist of *Lemur fulvus* during the support phase of a quadrupedal stride. Numbers refer to individual frames recorded on videotape where each frame represents 1/30 second. In frontal view (top row) arrows point to abducted (frame 1) and adducted (frame

6) positions of the forearm relative to the planted hand during the support phase. In lateral view (bottom row), arrows point to the extended position of the antebrachio-carpal joint (frame 10) and metacarpophalangeal joint (frame 17) during the support phase.

performed on log-transformed values of carpal shape ratios. Multivariate analysis of angular variables was performed on log-transformed angular values. Only those measurements found to be significant in bivariate and univariate statistical tests were included in these multivariate analyses. Summary statistics for linear measurements, articular arc lengths, and articular arc curvatures are provided in Table 2. Statistical tests were completed using the SYSTAT statistics software package.

RESULTS

Use and posture of the lemuriform wrist

***Lemur fulvus* (AAQ).** Lemurid positional behaviors are the most well documented of the Malagasy primates. *Lemur fulvus* and *Lemur variegatus* use leaping most often as a mode of locomotion, with quadrupedalism being the next most frequent pattern and climbing the least common (Dagosto, 1994). All three lemurid species studied here use horizontal supports in the majority of cases (Tattersall, 1982; Dagosto, 1994; Table 1). *Lemur catta* is unique among Malagasy primates in that it spends a considerable amount of time on the ground. Ward and Sussman (1979) estimate roughly 30% of its daily hours are spent terrestrially and 65% of group travel is done on the ground. Furthermore, Ward and Sussman (1979) never observed *L. catta* using vertical clinging postures. The frequent use of horizontal sub-

strates in all species of the genus *Lemur* highlights the role of the wrist joints as compressive weight-bearing units in this family. Moreover, the relatively infrequent use of vertical substrates by these three *Lemur* species emphasizes the habitual pronograde posture of these species during locomotion.

Movements at the lemurid wrist during quadrupedal strides are shown for *Lemur fulvus* in both lateral and frontal views (Fig. 3). Lateral views of these sequences show that the digits, and not the palm of the lemurid hand, contact the substrate first. This pattern of digitigrade touchdown is also observed in arboreal cercopithecines (Whitehead, 1993). The volar surfaces of phalanges II–V make initial contact with the support, and the hypothenar pad touches the substrate prior to midstance (Fig. 3, frame 3). The hypothenar and thenar pads remain in contact with the substrate for the majority of support phase until lift-off (Fig. 3, frame 13). These observations indicate that for the majority of support phase the planted hand is fully palmigrade with extension occurring at the antebrachio-carpal joint (Fig. 3, frame 10). At lift-off the palm is raised along with the metacarpals, and the metacarpophalangeal joints are extended (Fig. 3, frame 17). The hand briefly assumes a digitigrade posture at the end of the support phase (Fig. 3, frame 17).

These lateral views also show that, in *Lemur*, forward motion of the body mass over

the planted hand occurs by the body moving like an inverted pendulum (Hildebrand, 1985) anteriorly across the antebrachio-carpal joint, which acts as a pivot. The lemurid wrist is therefore 'carpi-fulcrumating,' in contrast to the wrists of many digitigrade cercopithecines, which are 'metacarpi-fulcrumating' (Nieschalk and Demes, 1993; Whitehead, 1993). Digits III–V of the lemurid hand contact the substrate first but also leave the substrate first as the forearm pronates toward the thenar border of the hand late in the support phase. Extension and pronation appear to occur simultaneously at the wrist of *Lemur fulvus* during the support phase of quadrupedal strides. Jenkins (1981) suggested that midcarpal pronation is likely to occur during above-branch, quadrupedal locomotion in primates. However, from cinematographic records it is not possible to know which joint contributes most to forearm pronation during quadrupedal walking in *Lemur*.

Frontal views of these locomotor sequences show that the hand is in a slightly ulnar deviated position and the forearm is abducted at initial touchdown (Fig. 3, frame 1). Following touchdown, the forearm is more adducted (radially deviated) relative to the planted hand, and reaches maximum adduction approximately at midstance (Fig. 3, frame 6). Following midstance the forearm is again slightly abducted relative to the fixed hand until the initiation of swing phase (Fig. 3, frame 13). These observations illustrate that the lemurid wrist experiences slight mediolateral excursions in the transverse plane during the support phase of quadrupedal strides. The proximal and midcarpal joints probably both contribute somewhat to these radioulnar movements. Forearm adduction and abduction at the wrist of *Lemur fulvus* take place while the wrist joints are transferring weight-bearing loads from the forearm to the hand (Yalden, 1972). The wrist must therefore be stabilized at the extreme medial and lateral limits of these movements in order to provide a firm articulation and resist joint displacement.

***Propithecus verreauxi* (VC).** The indriids are classic examples of 'vertical clingers and leapers' after Napier and Walker (1967)

and Napier (1967). Indriid leaping is described as ricochet between vertical substrates of large diameter, and bipedal hopping during occasional forays to the ground (Walker, 1979; Tattersall, 1982; Oxnard et al., 1990). Postural behaviors described for these genera include frequent clinging to upright supports and occasional sitting in the forks of trees (Walker, 1974, 1979; Tattersall, 1982; Oxnard et al., 1990). This is the same description given by Walker (1979) for *Avahi* and *Lepilemur*, and no other information is available for these two genera. *Propithecus* has been described as having a more varied locomotor and postural pattern than the other indriid genera (Walker, 1979; Tattersall, 1982). Leaping between vertical supports is also common in this indriid, but some quadrupedalism, climbing, bimanual and trimanual suspension, and even rare bouts of bimanual suspensory locomotion have also been observed for *Propithecus* (Walker, 1974, 1979; Gebo, 1987).

Captive *Propithecus verreauxi* individuals observed in the course of this study typically flex the proximal wrist joints when clinging to vertical substrates (Fig. 4A). On both large and relatively small supports the thumb is held divergent relative to rays II–V (Fig. 4A; Hamrick, in prep.). The hand itself is held in a supinated position, as one would hold it when 'shaking hands' (Fig. 4A). Additional postures observed in these captive individuals include antipronograde suspension on horizontal substrates, in which the wrist is again flexed and partially supinated (Fig. 4B). Quadrumanual and trimanual suspensory postures were also observed in several instances (Fig. 4C). During these below-branch behaviors a hook-grip is used where the hand is again partially supinated and the wrist and digits are flexed about the superstrate (Fig. 4C).

Previous authors have noted that the hand of *Propithecus* is well adapted for hanging and feeding from terminal branches (Bishop, 1964; Jolly, 1966; Cartmill, 1974). The use of the *Propithecus* forelimb in suspensory postures is particularly interesting from a functional standpoint. Supination of the forelimb and flexion at the wrist during these below-branch postures is quite similar to that observed during vertical clinging, al-

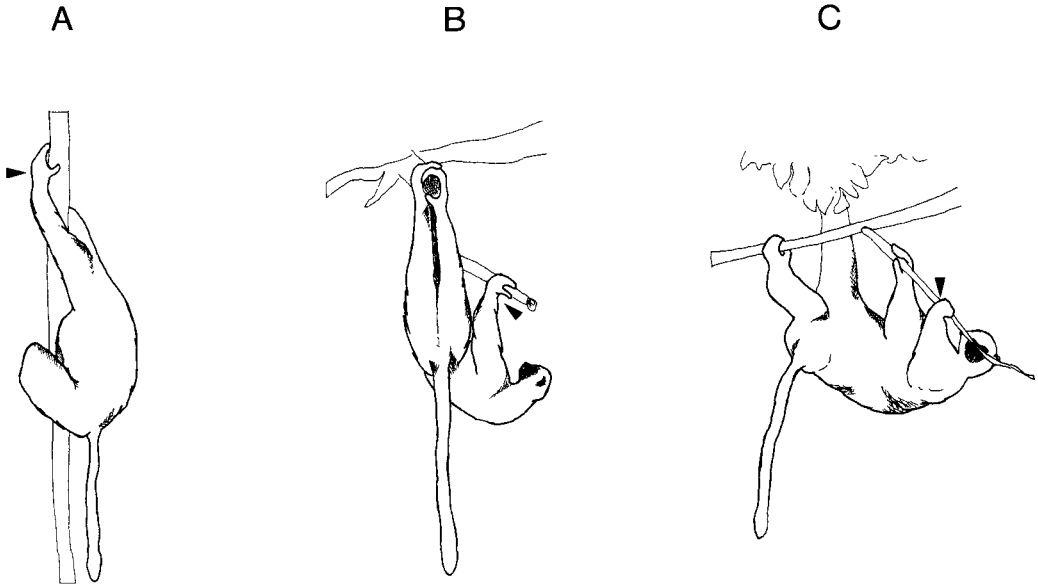


Fig. 4. Postures of the hand and wrist in *Propithecus verreauxi* during (A) vertical clinging, (B) suspensory, and (C) antipronograde postures. Arrows point to supinated (A) and flexed (B, C) positions of the wrist.

though the thumb is held alongside the other digits during forelimb suspensory postures whereas it is quite divergent during vertical clinging (Fig. 4). Naturalistic studies show that trimanous suspensory postures, in which the animal hangs from one hand and both feet, are quite common in both *L. variegatus* and *Propithecus* whereas bimanual suspension is much less frequent (Dagosto, pers. comm.). Nonetheless, similarities in hand postures observed in *Propithecus* during clinging and suspensory postures demonstrate that vertical clinging and hang-feeding are likely to require similar structural adaptations for wrist joint flexion and supination. However, these behaviors probably require different stabilizing mechanisms at the wrist since the distribution of forces would be different for each behavior.

Osteoligamentous morphology of the lemuriform wrist

The proximal joints. The inferior radioulnar joint of all lemuriforms examined is a syndesmosis, that is, the distal radius and ulna are united by a fibrous interosseous ligament. This joint morphology contrasts

with the condition found in many ceboid and cercopithecoid primates, in which an incipient synovial cavity is formed between the ulnar head and radial facet (Lewis, 1974, 1989). The synovial inferior radioulnar joint permits a considerable range of pronation and supination, whereas the syndesmosis of lemurs allows only slight mobility between the distal forelimb elements. These observations suggest that the wrists of both AAQs and VCs possess very limited potential for forearm rotation at the inferior radioulnar joint, considerably less than those of many anthropoid primates. Despite frequent supination of the hand by VCs, the inferior radioulnar joints of these taxa do not appear capable of any more axial rotation than those of AAQs. It should be noted that in a few skeletal specimens of *Propithecus verreauxi* the radial facet for the ulnar head is quite concave, suggesting that in some cases an incipient synovial cavity may develop.

The proximal wrist joint of lemuriforms consists of two compartments, radiocarpal and ulnocarpal, divided by a strong ligamentous longitudinal septum which attaches to the lunate and triquetrum (Fig. 5). This

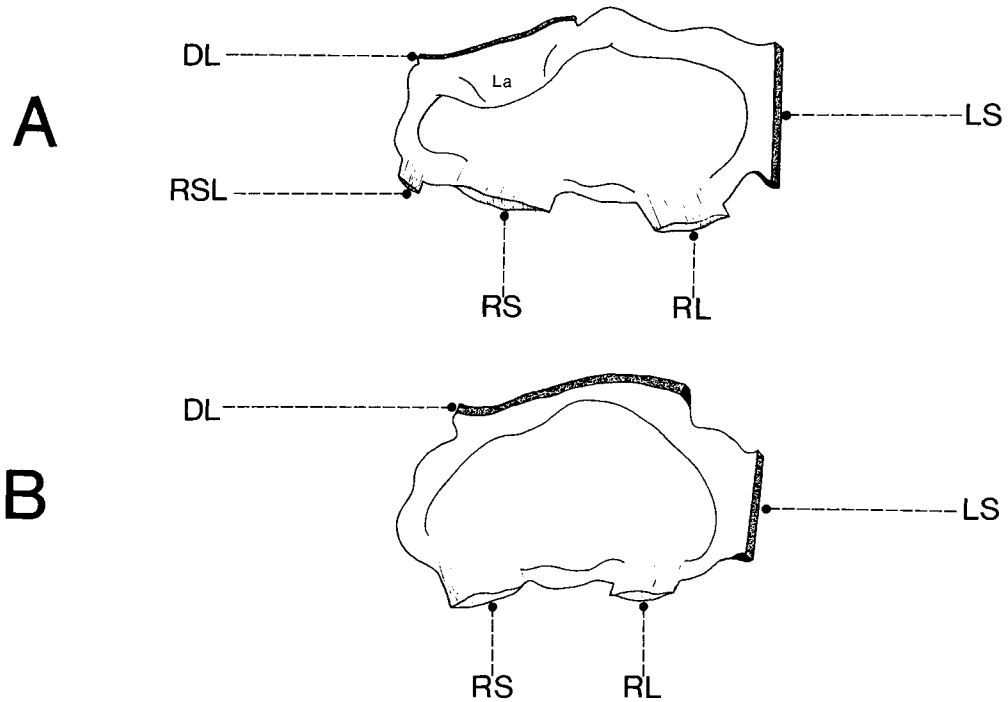


Fig. 5. Distal view of the distal radius and radiocarpal ligaments in (A) *Lemur fulvus* and (B) *Avahi laniger*. Abbreviations: DL, dorsal radiocarpal ligament; La, intraarticular labrum; RSL, radial stylo-carpal ligament; RS, volar radio-scaphoid ligament; RL, volar radio-lunate ligament; LS, longitudinal ligamentous septum.

thick banded ligament prevents the proximal row from sliding either medially or laterally across the distal radius, and therefore limits the potential range of radioulnar deviation. The triquetrum is held rigidly in place by the septum attaching laterally and an ulnotriquetral ligament attaching medially (Fig. 5). Manipulation of preserved osteoligamentous preparations shows that very little mediolateral deviation is possible at the ulnocarpal joint due to the presence of these ligaments, although a considerable range of flexion and extension is possible. The majority of ulnar deviation, as well as the majority of wrist rotation, was observed in ligamentous preparations to occur at the midcarpal joint.

Godinot and Beard (1991, p. 314) noted that notharctines possess a "nonarticular bony process of unknown function" tapering medially (ulnarly) from the triquetrum. Lemuriforms also possess this bony process,

which does not articulate with the ulna but instead embraces the dorsal bony of the pisiform (Fig. 6b). This bony flange is bound tightly to the pisiform by the ulnospisiform ligament, and is also tethered securely to the distal ulna by the ulnotriquetral ligament. This osteoligamentous arrangement creates an extremely stable configuration for the tip of the ulna, and in fact restricts any ulnar deviation at the ulnocarpal joint. The medial 'flange' does not articulate with the ulna's ulnocarpal facet, but rather serves as a bony anchor for the medial ulnocarpal ligaments.

The dorsal ligamentous capsule of AAQs bears an intracapsular fold of synovial tissue, or labrum, on the inner portion of the radiocarpal ligament. This labrum is visible when the capsule is opened dorsally (Fig. 5A). The fold exists as a slight cushion interposed between the dorsal radius and radial styloid proximally and a depression on the scaphoid distally. Manipulation of preserved

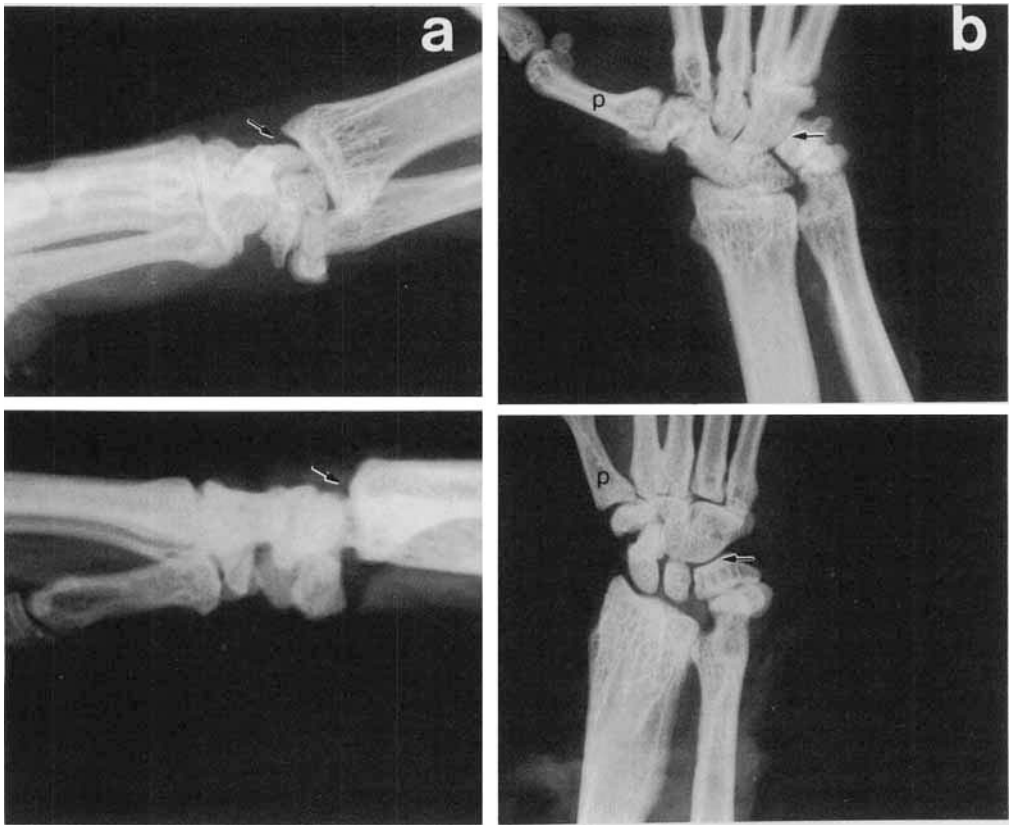


Fig. 6. Lateral (a) and dorsal (b) radiographs of the wrist in *Lepilemur mustelinus* (top row) and *Lemur fulvus* (bottom row). Arrows in (a) point to the dorsoventrally curved and anteriorly tilted radiocarpal articulation of *Lepilemur* (top) and dorsoventrally flattened radiocarpal articulation of *Lemur* (bottom). Arrows in (b) point to the midcarpal joint of *Lepilemur* (top) and *Lemur* (bottom), showing the triquetrohamate articulation. Note also the divergent pollex (p) of *Lepilemur* (b; top row).

osteoligamentous preparations demonstrates the intraarticular labrum is contacted and compressed when the lemurid wrist is extended and pronated in the quadrupedal position. The AAQ distal radius is quite flat dorsoventrally (Fig. 6a), and rests on the dorsal and anterior margin of the scaphoid during extension. The dorsal capsules of those VCs examined differ from all three AAQ species in lacking this fold, and correspondingly lacking a depression on the scaphoid for the dorsal radius (Fig. 5B).

In contrast to the AAQs, *Avahi*, *Lepilemur*, and *Propithecus* possess an extremely thick, fibrous, dorsal radiocarpal ligament (Fig. 5B). This ligament originates from a very large dorsal radial tubercle and inserts on

the dorsal edges of the scaphoid, lunate, and triquetrum. No triquetral insertion of this ligament was observed in lemurids. This dorsal radiocarpal ligament is taut during flexion of the proximal wrist joint (see Fig. 8), and stabilizes the proximal carpal row against dorsal displacement during radiocarpal flexion. The radiocarpal joint of VCs, in contrast to that of AAQs, is deeply curved and tilted anteriorly, which both increases the degree of wrist flexion and stabilizes the joint during radiocarpal flexion (Fig. 6a). The lunate is displaced palmarly in VCs, and the opposing joint surfaces are congruent when the wrist is held in a flexed position. This configuration makes a stable flexed position of the radiocarpal joint an important

working position of the hand, which is not surprising given the fact that the wrist joint of VCs is most often flexed during vertical clinging and hang-feeding postures (Fig. 4).

The palmar capsule of the lemuriform specimens examined is quite similar, with the exception of a small ligament from the radial styloid to scaphoid present in all three AAQs. A volar ligamentous attachment from the radial styloid to the scaphoid was not observed in *Avahi* and *Propithecus*, and only a small portion was seen in a single specimen of *Lepilemur* (Fig. 5B). The volar radiocarpal ligaments are stressed under tension during extension of the joint (Tuttle, 1967; see also Fig. 8), and the well-developed palmar radiocarpal ligaments of AAQs stabilize the proximal joint against radiocarpal displacement during extension. The dorsal intraarticular labrum and radial stylocarpal ligament of AAQs and thick fibrous dorsal radiocarpal ligament of VCs reflect two contrasting patterns of antebrachicarpal movement in lemuriforms, namely extension in arboreal quadrupeds and flexion in vertical clingers.

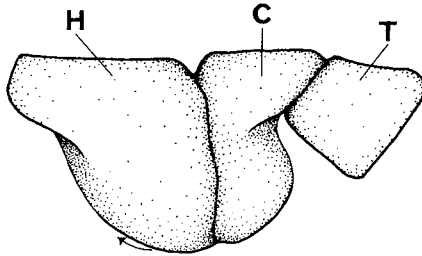
The distal joints. The midcarpal joints of *Lemur fulvus*, *Lemur variegatus*, and *Lemur catta* are all quite similar and reflect a very basic arrangement common in many quadrupedal monkeys (Fig. 6b). Preserved hand specimens of these three species were manipulated in ulnar deviation, extension, and pronation, in order to identify the range of midcarpal movements possible in lemuriform AAQs. As mentioned above, and also by Hughes (1944), ulnar deviation occurs primarily at the lemuriform midcarpal joint. When the hand is manipulated to assume an ulnar deviated and extended posture, the ulna pushes the triquetrum against the hamate's triquetral facet, which is directed somewhat proximally in a weight-bearing orientation (Figs. 6b, 7A). The triquetrum then courses distally and palmarly against the hamate 'spiral' facet, so the midcarpal joint is ultimately impacted in an extended and slightly pronated position. The AAQ capitate-trapezoid embrasure for the *os centrale* is also widest on its dorsal side, and the capitate facet for the *os centrale* faces slightly dorsally (Fig. 7A). These two features allow the proximal carpal row to be

pronated (rotated palmarly) into the capitate-trapezoid trough from the neutral position. Similar features were observed by Jenkins (1981) to allow 'hyperpronation' at the midcarpal joint of *Macaca*.

The midcarpal articulation is quite different in the vertical clingers examined. The hamate's triquetral facet is directed more distally in VCs (Fig. 6b, 7B), which in preserved specimens allows an increased range of midcarpal ulnar deviation compared to that of AAQs. The capitate-trapezoid notch for the *os centrale* is wide on its palmar side and constricted dorsally in VCs, and the capitate facet for the *os centrale* faces more laterally than dorsally (Fig. 7B). The configuration of the capitate-trapezoid trough in VCs does not permit the proximal row and *os centrale* to be pronated (rotated palmarly) easily about the fixed distal row. Rather, the dorsally constricted notch of VCs enables the proximal carpal row to be more easily supinated (rotated dorsally) into the capitate-trapezoid trough from the neutral position. A laterally facing capitate head and dorsally constricted capitate-trapezoid embrasure were also shown by Jenkins (1981) to allow a greater range of midcarpal supination in *Ateles* and *Hylobates*.

Midcarpal movements in Malagasy primates are visualized more easily if the distal carpal row and digits are considered as one functional unit, and the proximal carpal row and radius are viewed as a separate functional unit (Fig. 8). During the support phase of quadrupedal strides the planted hand is essentially fixed while the hand maintains a grasp. The forearm is extended over the proximal carpal row (Fig. 8A), but this joint allows no rotation. Therefore, as the radius is pronated about the ulna at the radioulnar joints, the radius carries with it the proximal carpal row. This radioulnar pronation causes the proximal carpal row itself to be pronated about the fixed distal carpal row (Fig. 8A). In a similar fashion, the hand of a VC is fixed as it grasps a vertical substrate. The radiocarpal joint is flexed, but this joint again allows no rotation (Fig. 8B). The radius is slightly supinated about the ulna at the radioulnar joints, and the radius carries with it the proximal carpal row (Fig. 8B). This radioulnar supination moves the proxi-

(A)



(B)

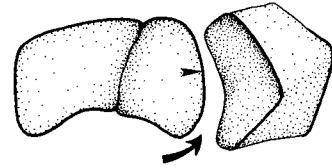
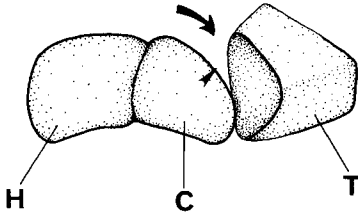
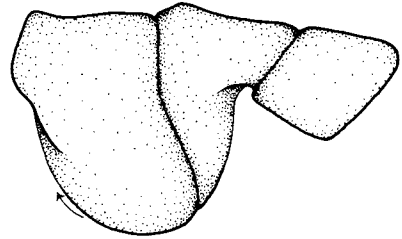


Fig. 7. **Top row:** Dorsal view of the left midcarpal articular surface in an active arboreal quadruped, *Lemur variegatus* (A), and a vertical climber, *Avahi laniger* (B). Note the more proximally facing triquetrohamate facet of *Lemur* (A; curved arrow) and more distally directed facet of *Avahi* (B; curved arrow). Note also the mediolaterally expanded capitate head of *Lemur* and mediolaterally compressed head of *Avahi*. **Bottom row:** Proximal view of the left midcarpal articular surface in *Lemur variegatus* (A) and *Avahi laniger* (B). Note the

dorsally expanded capitate-trapezoid embrasure (A; large arrow) and dorsally facing capitate articular surface (A; arrowhead) of *Lemur*. In contrast, the capitate-trapezoid embrasure is expanded palmarly (B; large arrow) and constricted dorsally in *Avahi*, and the capitate facet faces laterally (B; arrowhead). The large arrows indicate movement of the proximal carpal row about the fixed distal carpal row. H, hamate; C, capitate; T, trapezoid. Not drawn to scale.

mal carpal row itself into a somewhat supinated position about the fixed distal carpal row. These simplified models (Fig. 8) illustrate the basic mechanisms by which radiocarpal extension and midcarpal pronation occur in arboreal quadrupeds, and radiocarpal flexion and midcarpal supination occur in vertical clingers.

Carpal osteometrics of lemuriform primates

The proximal joints. Linear regressions indicate all linear carpal dimensions examined in this study are highly correlated with overall size of the wrist complex, and among

lemuriforms breadth of the ulnar head is strongly correlated with both of the size variables included in this study (Table 3). ANCOVAs demonstrate that, relative to carpal size, VCs and AAQs do not differ significantly in breadth of the ulnar head (Table 4). Relative to estimated body size, AAQs are observed to have a slightly larger ulnar head than VCs. These results are surprising given that previous workers (Corruccini et al., 1975; O'Connor, 1975; Corruccini, 1977) have related a large ulnar head to an increased range of inferior radioulnar supination during orthograde climbing and suspensory postures. Results presented here, along

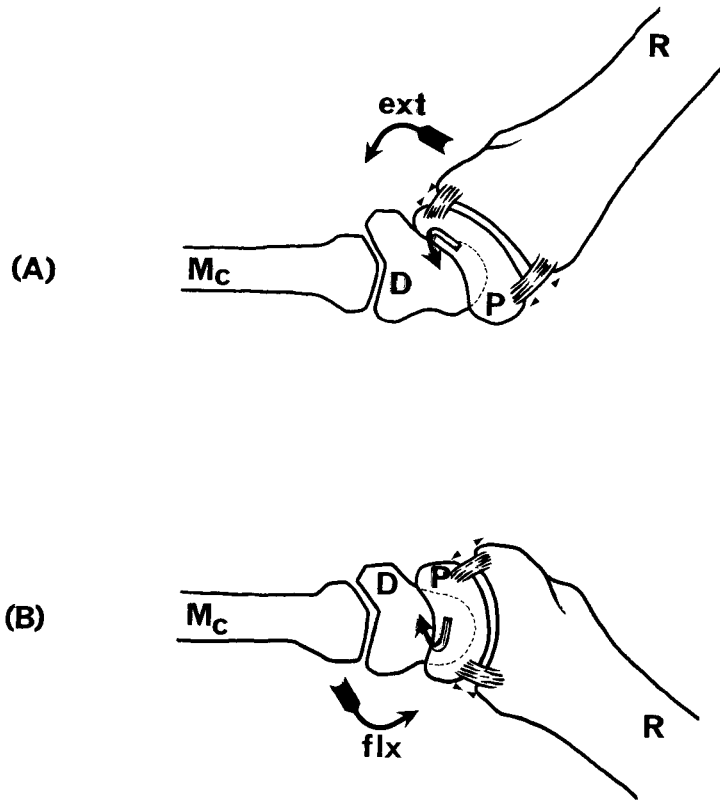


Fig. 8. Schematic representation of carpal joint movements in an active arboreal quadruped (A) and vertical clinger (B). A right hand is illustrated in medial view, and is shown as if a sagittal section were taken along the long axis of the third metacarpal (Mc). During the support phase of a quadrupedal stride (A) the radius (R) moves anteriorly on the proximal carpal row (P) in extension (ext), and the proximal carpal row (P) is pronated about the fixed distal carpal row (D). In con-

trast, the radiocarpal joint is flexed (flx) when the hand grasps a vertical support (B), and the proximal carpal row (P) is slightly supinated about the fixed distal carpal row (D). The dorsal radiocarpal ligament experiences compression when the radiocarpal joint is extended (A), but experiences tension when the joint is flexed (B). The palmar radiocarpal ligament experiences tension when the radiocarpal joint is extended (A), but undergoes compression during radiocarpal flexion (B).

with those discussed previously, demonstrate that VCs do not have a broader ulnar head or more mobile inferior radioulnar joint than AAQs despite gross differences in hand postures and wrist joint kinematics.

Metric data do however show clear evidence of morphoclines between VCs and AAQs in several aspects of antebrachio-carpal joint morphology. VCs have a radiocarpal articular facet that is very curved dorsoventrally (Tables 2, 5; Figs. 6a, 9a), in contrast to AAQs which possess a radiocarpal facet that is much more flat dorsoventrally (Tables 2, 5; Figs. 6a, 9a). As noted earlier, the deeply curved and anteriorly tilted radiocar-

pal facet of VCs (Tables 2, 5; Fig. 6a, 9a) stabilizes the proximal wrist joint during flexion but limits the range of antebrachio-carpal extension. The flatter radiocarpal facet of *Lemur* (Table 2) is more stable under unidirectional weight-bearing, whereas a curved facet is more stable through a wider range of parasagittal joint movements (Sarmiento, 1988). *Lemur fulvus* has a quite high degree of dorsopalmar curvature compared to other AAQs (Fig. 9a; Table 2), possibly because it practices vertical clinging more frequently than *L. variegatus* (Dagosto, 1994) and *L. catta* (Ward and Sussman, 1979).

TABLE 3. Bivariate regression analyses of osteological measurements against two different size variables, humeral midshaft breadth and carpal size

Measurement ^a	Y intercept ^b	Slope ^b	r ^c
Ulnar head width (1)	.06/- .42 (-.03/- .6)	1.1/1.13 (1.15/1.24)	.95/.91
Ulnar styloid length (2)	-.40/- 1.01 (-.54/- 1.28)	1.3/1.36 (1.38/1.52)	.95/.89
Radial styloid length (3)	-.95/- 1.4 (-1.5/- 2.35)	1.29/1.27 (1.67/1.81)	.77/.70
Radial articular width (4)	.65/.14 (.57/- .01)	.99/1.06 (1.03/1.15)	.96/.92
Trapezium breadth (5)	.09/- .25 (-.08/- .62)	.97/.97 (1.11/1.19)	.87/.81
Trapezoid width (6)	-.44/- 1.03 (-.61/- 1.32)	1.07/1.16 (1.17/1.33)	.91/.87
Radius mediolateral arc length (a-b)	.62/.23 (.53/- .01)	.97/.98 (1.03/1.13)	.94/.86
Radius dorsoventral arc length (c-d)	.04/- .34 (-.15/- .64)	.89/.91 (1.01/1.08)	.88/.84
Scaphoid dorsoventral arc length (e-f)	.31/- .14 (.11/- .51)	.99/1.03 (1.12/1.24)	.88/.83
Midcarpal mediolateral arc length (g-h)	.91/.40 (.78/.13)	1.08/1.15 (1.17/1.30)	.92/.88
Radius mediolateral curvature (a-b)	3.25/3.5 (5.35/5.94)	-.08/- .21 (-1.6/- 1.61)	.05/.13 ns
Radius dorsoventral curvature (c-d)	4.4/4.92 (5.53/7.06)	-.80/- .96 (-1.73/- 2.18)	.46/.44 ns
Scaphoid dorsoventral curvature (e-f)	4.38/4.37 (5.03/5.28)	-.12/- .10 (-.60/- .62)	.20/.16 ns
Midcarpal mediolateral curvature (g-h)	4.49/4.56 (4.97/5.0)	-.001/- .02 (-.33/- .28)	.00/.07 ns

Results are given for regressions v. carpal size/regressions v. humeral midshaft diameter.
^aNumbers and letters in parentheses refer to measurements shown in Figure 1.
^bModel I (ordinary least squares [OLS]) values shown above, Model II (reduced major axis [RMA]) values shown below in parentheses.
^cRegressions are significant at $P < .001$ unless noted otherwise; ns = non-significant at $P < .05$. r here is the correlation coefficient.

TABLE 4. ANCOVA tests (vertical clingers vs. quadrupeds) for the measurements shown in Figure 1

Measurement ^a	Slope	Y intercept
Ulnar head width (1)	ns/ns	ns/* (quadrupeds >)
Ulnar styloid length (2)	*/ns	/* (quadrupeds >)
Radial styloid length (3)	*/ns	/* (quadrupeds >)
Radial articular width (4)	(vertical clingers >) ns/ns	*/ns (quadrupeds >)
Trapezium breadth (5)	ns/ns	*/ns (vertical clingers >)
Trapezoid width (6)	ns/ns	*/ns (quadrupeds >)
Distal radius mediolateral arc length (a-b)	***/* (quadrupeds >)	/* (quadrupeds >)
Distal radius dorsoventral arc length (c-d)	ns/ns	ns/ns
Scaphoid dorsoventral arc length (e-f)	ns/* (quadrupeds >)	ns/ (quadrupeds >)
Midcarpal mediolateral arc length (g-h)	ns/ns	ns/ns

ANCOVA test results are given for measurements v. carpal size/regressions v. humeral midshaft diameter.
^aNumbers and letters in parentheses refer to measurements shown in Figure 1.
*** $P < .001$; ** $P < .01$; * $P < .05$; ns = non-significant.

Dorsopalmar curvature of the scaphoid was also found to differ among the lemuriforms included in this study (Table 5). Pairwise comparisons demonstrate that these interspecific differences are observed primarily between *Lemur catta* and the other lemuriform species. *L. catta* possesses the flattest (dorsoventrally) scaphoid of the six

TABLE 5. Results of pairwise comparisons for joint curvature values between lemuriform species

Distal radius mediolateral included angle (a–b) ^a Kruskal-Wallis test statistic _(5 DF) = 19.76, <i>P</i> < .001						
	<i>Propithecus</i>	<i>Avahi</i>	<i>Lepilemur</i>	<i>L. variegatus</i>	<i>L. catta</i>	<i>L. fulvus</i>
<i>L. fulvus</i>	ns	ns	ns	ns	ns	—
<i>L. catta</i>	ns	ns	**	*	—	
<i>L. variegatus</i>	**	ns	ns	—		
<i>Lepilemur</i>	**	ns	—			
<i>Avahi</i>	ns	—				
<i>Propithecus</i>	—					
Distal radius dorsoventral included angle (c–d) Kruskal-Wallis test statistic _(5 DF) = 45.67, <i>P</i> < .001						
	<i>Propithecus</i>	<i>Avahi</i>	<i>Lepilemur</i>	<i>L. variegatus</i>	<i>L. catta</i>	<i>L. fulvus</i>
<i>L. fulvus</i>	ns	*	**	**	**	—
<i>L. catta</i>	***	***	***	ns	—	
<i>L. variegatus</i>	**	**	***	—		
<i>Lepilemur</i>	ns	*	—			
<i>Avahi</i>	ns	—				
<i>Propithecus</i>	—					
Scaphoid dorsoventral included angle (e–f) Kruskal-Wallis test statistic _(5 DF) = 16.83, <i>P</i> < .01						
	<i>Propithecus</i>	<i>Avahi</i>	<i>Lepilemur</i>	<i>L. variegatus</i>	<i>L. catta</i>	<i>L. fulvus</i>
<i>L. fulvus</i>	ns	ns	ns	ns	ns	—
<i>L. catta</i>	***	*	***	ns	—	
<i>L. variegatus</i>	ns	ns	ns	—		
<i>Lepilemur</i>	ns	ns	—			
<i>Avahi</i>	ns	—				
<i>Propithecus</i>	—					
Midcarpal mediolateral included angle (g–h) Kruskal-Wallis test statistic _(5 DF) = 16.44, <i>P</i> < .01						
	<i>Propithecus</i>	<i>Avahi</i>	<i>Lepilemur</i>	<i>L. variegatus</i>	<i>L. catta</i>	<i>L. fulvus</i>
<i>L. fulvus</i>	*	ns	ns	ns	ns	—
<i>L. catta</i>	**	*	ns	ns	—	
<i>L. variegatus</i>	ns	ns	ns	—		
<i>Lepilemur</i>	ns	ns	—			
<i>Avahi</i>	*	—				
<i>Propithecus</i>	—					

^a Letters in parentheses refer to measurements shown in Figure 1.

Significance level for pairwise comparisons (Kolmogorov-Smirnov two-sample test): ****P* < .001; ***P* < .01; **P* < .05; ns = non-significant.

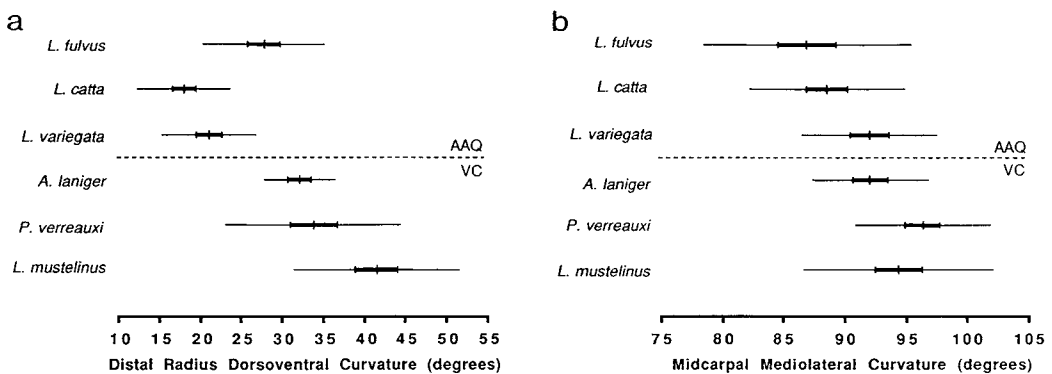


Fig. 9. Univariate plots showing values for dorsoventral curvature of the distal radius (a) and medio-lateral curvature of the midcarpal joint (b) in lemuriforms. The thin vertical line is the mean, the thick horizontal line is one standard error, and the thin horizontal line is one standard deviation. AAQ, active arboreal quadrupeds; VC, vertical clingers.

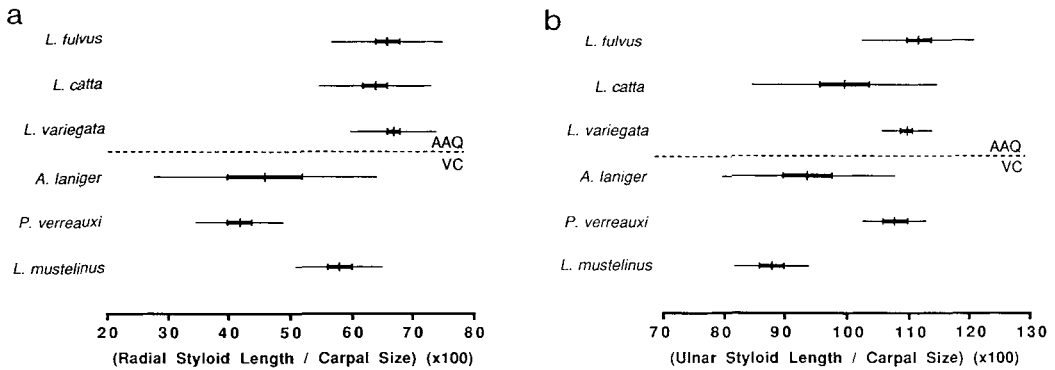


Fig. 10. Univariate plots showing ratio values for relative radial styloid length (a) and relative ulnar styloid length (b). The thin vertical line is the mean, the thick horizontal line is one standard error, and the thin horizontal line is one standard deviation. AAQ, active arboreal quadrupeds; VC, vertical clingers.

species included for analysis (Tables 2, 5). The flatter shape of the scaphoid's radiocarpal articular surface is related to the role of the radiocarpal joint in unidirectional weight-bearing during quadrupedal postures (Sarmiento, 1988). The flatter proximal wrist joint of *L. catta*, specifically the dorsoventrally flat distal radius and proximal scaphoid, stabilizes the radiocarpal joint during quadrupedal postures on arboreal and terrestrial substrates. It is also worth noting that dorsopalmar curvature of the lunate mimics that of the scaphoid, although lunate shape was not quantified in this study.

Shape ratios (Fig. 10; Table 6) and ANCOVAs (Table 4) also show that AAQs have relatively longer radial and ulnar styloids than VCs. Pairwise comparisons show a particularly strong contrast between AAQs and VCs in relative length of the radial styloid (Fig. 10a; Table 6). Well-developed radial and ulnar styloids stabilize the antebrachiocarpal joint against joint displacement when weight is being transferred from the forearm to the carpus during the support phase (Tuttle, 1967; Sarmiento, 1988). As noted earlier, this weight transfer occurs in AAQs as the forearm moves transversely across the wrist (Fig. 3), which requires a very firm articulation at the radial and ulnar margins of the proximal wrist joint so that the articulation remains stable throughout the deviational range (Yalden, 1972). Decreased transverse radiocarpal curvature and expanded trans-

verse radiocarpal breadth are features also considered to increase mediolateral stability at the proximal wrist joint (Fleagle and Meldrum, 1988; Sarmiento, 1988). *Lepilemur* and *L. variegatus* have the greatest degree of mediolateral radiocarpal curvature whereas *Propithecus* and *L. catta* have the least (Tables 2, 5). These data show no evidence of a morphocline between VC and AAQ lemuri-forms in relative degree of transverse radiocarpal curvature. Likewise, ANCOVAs (Table 4) show few differences between AAQs and VCs in mediolateral breadth of the radiocarpal articulation.

Propithecus does not differ significantly from AAQs in the relative length of its ulnar styloid (Table 6; Fig. 10b). *Propithecus* is also the only VC which lacks a fused *os centrale*, again resembling AAQs in this respect. The relatively longer ulnar styloid of *Propithecus* could be viewed as a primitive retention from an 'AAQ-like' ancestor, or might be related functionally to some as yet undefined aspect of its positional behavior which requires additional ulnocarpal stability. *Lemur catta* differs from other AAQs in having a relatively short ulnar styloid (Fig. 10). This difference between the ringtailed lemur and other AAQs could be related to the more terrestrial affinities of this species. Primates which move on small diameter arboreal supports tend to abduct the limbs more so than those moving on terrestrial or large diameter supports (Meldrum, 1991). Forelimb abduction helps to reduce transverse substrate re-

TABLE 6. Results of pairwise comparisons for ratio values between lemuriform species

Radial styloid length/carpal size Kruskal-Wallis test statistic _(5, DF) = 32.03, $P < .001$						
	<i>Propithecus</i>	<i>Avahi</i>	<i>Lepilemur</i>	<i>L. variegatus</i>	<i>L. catta</i>	<i>L. fulvus</i>
<i>L. fulvus</i>	**	**	*	ns	ns	—
<i>L. catta</i>	***	**	ns	ns	—	
<i>L. variegatus</i>	***	**	**	—		
<i>Lepilemur</i>	**	ns	—			
<i>Avahi</i>	ns	—				
<i>Propithecus</i>	—					
Ulnar styloid length/carpal size Kruskal-Wallis test statistic _(5, DF) = 30.78, $P < .001$						
	<i>Propithecus</i>	<i>Avahi</i>	<i>Lepilemur</i>	<i>L. variegatus</i>	<i>L. catta</i>	<i>L. fulvus</i>
<i>L. fulvus</i>	ns	*	***	ns	ns	—
<i>L. catta</i>	ns	ns	**	ns	—	
<i>L. variegatus</i>	ns	**	***	—		
<i>Lepilemur</i>	***	*	—			
<i>Avahi</i>	**	—				
<i>Propithecus</i>	—					

Significance level for pairwise comparisons (Kolmogorov-Smirnov two-sample test): *** $P < .001$; ** $P < .01$; * $P < .05$; ns = non-significant.

action forces on the forelimb joints (Schmitt, 1993), and keeps the body's center of mass closer to the substrate to avoid falling off or pitching over (Napier, 1967; Cartmill, 1985). Primates such as terrestrial cercopithecines, which move with more upright, adducted limb postures (Meldrum, 1991), align the forearm in the sagittal plane and thus towards the radial margin of the wrist. The shorter ulnar styloid and robust radial styloid of *Lemur catta* (Fig. 10) may be related to more adducted postures of the forelimb in this species during quadrupedal terrestrial locomotion.

Multivariate discriminant analyses also demonstrate that linear and angular dimensions of the lemuriform proximal wrist joints distinguish VCs from AAQs. The discriminant analysis using shape ratios is highly significant ($P < .001$, Wilkes-Lambda), and classified 95% of the cases correctly (Fig. 11A). The first discriminant function separates the VCs from AAQs, and is most highly correlated with radial styloid length (Fig. 11A; Table 7). A bivariate plot of the first two discriminant axes shows that the AAQs have positive factor scores on this axis, and relatively long radial styloids, whereas the vertical clingers have negative scores, and relatively shorter radial styloids (Fig. 11A). The analysis using angular variables is also highly significant ($P < .001$, Wilkes-Lambda), and classified over 90% of the cases correctly (Fig. 11B). The first discrimi-

nant function separates the VCs from AAQs, and is most highly correlated with dorsoventral curvature of the distal radius (Fig. 11B; Table 7). A plot of the first two discriminant axes shows that the VCs have positive scores on this axis, and a high degree of dorsoventral radiocarpal curvature, whereas the AAQs have negative factor scores on this axis, and a lower degree of dorsoventral radiocarpal curvature (Fig. 11B). These multivariate results underscore those conclusions derived from univariate and bivariate analyses, namely that the proximal wrist joints of AAQs differ from those of VCs in relative radial styloid length and dorsoventral curvature of the radiocarpal articulation.

The distal joints. Interspecific comparisons of lemuriform midcarpal joint dimensions also provide strong evidence for morphoclines in wrist joint morphology between AAQs and VCs. The midcarpal surface of vertical clingers is very curved with a high included angle, in contrast to the AAQs which in general have a flatter midcarpal articulation (Tables 2, 5; Figs. 6b, 9b). The low degree of midcarpal curvature observed in AAQs is due to their triquetrohamate facet being directed proximally in a weight-bearing attitude (Fig. 7A). The more proximally facing triquetrohamate facet of AAQs enables the midcarpal joint to support weight-bearing loads transmitted from the forelimb during quadrupedal postures

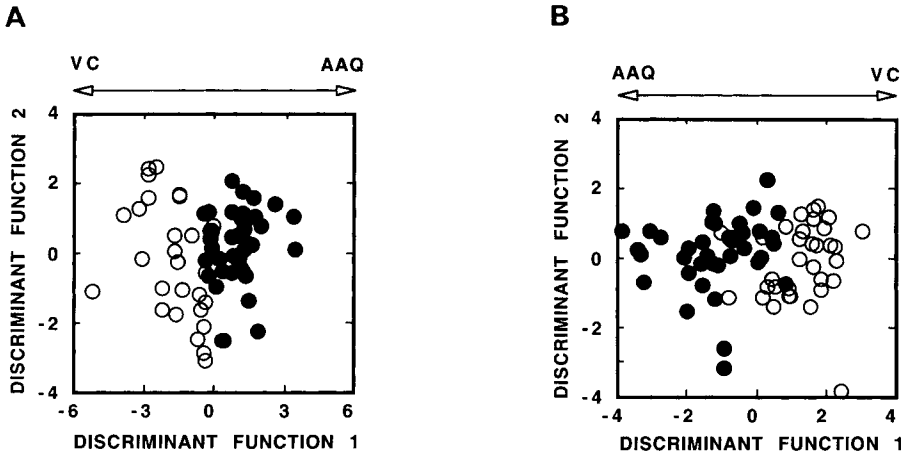


Fig. 11. Bivariate plots of the first two discriminant axes for (A) discriminant analysis of log-carpal shape ratios and (B) discriminant analysis of log-joint curvatures. Closed circles are active arboreal quadrupeds (AAQ) and open circles are vertical clingers (VC).

TABLE 7. Correlations (loadings) between shape variables and the first three discriminant function axes (factors) for discriminant analysis of lemuriform wrist joint log-shape ratio (shape variable) and log-curvature (subtended angle) values

	Factor 1	Factor 2	Factor 3
Shape variable			
Radial styloid length (3)	.61	-.24	-.34
Trapezoid breadth (6)	.56	-.19	.54
Ulnar styloid length (2)	.29	.70	-.48
Ulnar head breadth (1)	.26	.30	.60
Trapezium breadth (5)	-.25	.17	-.12
Radius articular breadth (4)	-.08	-.04	-.56
Subtended angle			
Radius dorsoventral curvature (c-d)	.51	-.02	-.84
Midcarpal mediolateral curvature (g-h)	.38	-.30	.85
Scaphoid dorsoventral curvature (e-f)	.38	-.03	-.16
Radius mediolateral curvature (a-b)	.04	.97	-.22

Numbers and letters in parentheses refer to measurements shown in Figure 1.

(Lewis, 1974; Jenkins and Fleagle, 1975; Fleagle, 1977; Sarmiento, 1988). In contrast, a very curved midcarpal joint allows a greater range of radioulnar deviation and is less stable under compressive, unidirectional, weight-bearing loads (Yalden, 1972; Sarmiento, 1988). ANCOVAs (Table 4) show that, relative to carpal size, length of the midcarpal articular arc does not differ significantly between VCs and AAQs. Hence, the principal morphological change which affects variation in the range of radioulnar motion at the lemuriform midcarpal joint involves altering joint curvature rather than arc length.

Lemur variegatus has a very high degree of midcarpal curvature compared to other AAQs (Table 2; Fig. 9b). This species is the largest of the lemurids and, all else being equal, should therefore place the largest compressive weight-bearing loads on the carpal joints. Dagosto (1994) has shown that this species uses suspensory postures significantly more than either *L. fulvus* or *L. rubriventer*. In fact, suspensory postures represent over 30% of the postural bouts observed for *L. variegatus* whereas suspension represents less than 5% of the postural bouts observed for either *L. fulvus* or *L. rubriventer* (Dagosto, 1994). The most plausible expla-

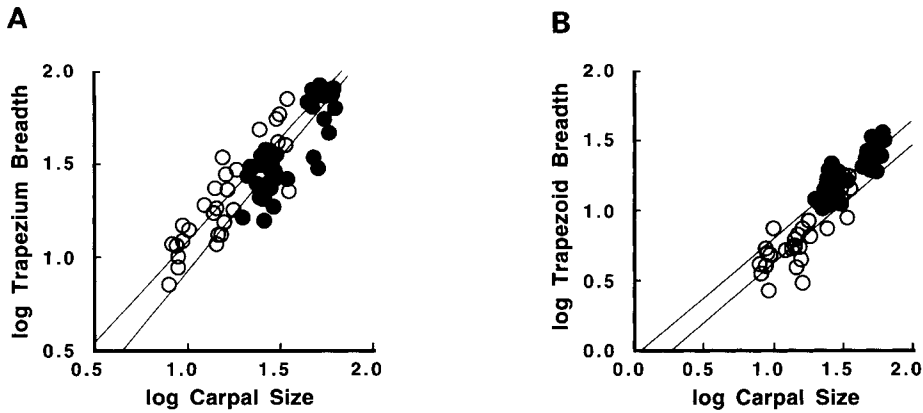


Fig. 12. Bivariate plots of log-trapezium breadth (A) and log-trapezoid breadth (B) against log-carpal size. Closed circles are active arboreal quadrupeds, open circles are vertical clingers, and the oblique lines represent ordinary least square (OLS) regression lines.

nation for the more curved midcarpal surface of *L. variegatus* is that this species practices more suspension than the other lemuriform AAQs, and therefore loads the midcarpal joint in quadrupedal weight-bearing postures less frequently than other lemuriform AAQs.

Finally, at the pollical margin, linear metrics demonstrate the trapezium of VCs is proportionately larger relatively to overall carpal size than that of AAQs (Fig. 12A). Lemuriform VCs have a powerful, divergent thumb which is used to securely grasp arboreal supports during prolonged clinging postures (Cartmill, 1974). Contraction of the thenar muscles during pollical grasping produces considerable transarticular compressive forces across the pollical carpometacarpal joint. Expanding the area of contact at the first carpometacarpal joint increases the bearing area, and therefore reduces joint stress, during pollical grasping. ANCOVAs (Table 4) also show that AAQs have a larger trapezoid than VCs relative to carpal size (Fig. 12B). The relatively smaller trapezoid of VCs is probably due to spatial constraints, that is, the trapezoid is reduced to accommodate the expanded trapezium. The trapezoid of AAQs is probably also expanded somewhat to reduce joint stress at the second carpometacarpal joint when the hand assumes a digitigrade posture late in the support phase (Fig. 3). Thus, VCs are characterized

by an expanded pollical carpometacarpal articulation and hypertrophied trapezium whereas AAQs have a relatively larger trapezoid and less expanded pollical carpometacarpal joint (Table 4; Fig. 12). These results support the hypothesis of Van Horn (1972) that primates which climb and cling to vertical arboreal supports require a powerful thumb to grasp vertical substrates.

Multivariate analyses also demonstrate that both linear and angular dimensions of the lemuriform midcarpal and pollical carpometacarpal joints distinguish VCs from AAQs. The first axis of the discriminant analysis using log-shape ratios separates VCs from AAQs (Fig. 11A), and is highly correlated with breadth of the distal trapezoid surface (Table 7). A bivariate plot of the first two discriminant axes shows that AAQs have positive factor scores, and a wide trapezoid, whereas the VCs have negative factor scores, and a relatively narrower trapezoid (Fig. 11A). The first axis of the discriminant analysis using logged angles also separates VCs from AAQs (Fig. 11B), and is highly correlated with mediolateral curvature of the midcarpal articulation (Table 7). A bivariate plot of the first two discriminant axes shows that VCs have positive factor scores, and a very curved midcarpal surface, whereas the AAQs have negative factor scores, and a comparatively flatter midcarpal surface (Fig. 11B). These multivariate results

provide further evidence that VCs and AAQs differ in morphology of both the midcarpal and carpometacarpal articulations.

DISCUSSION

Wrist morphology and vertical posture in arboreal primates

The preceding results suggest significant contrasts in carpal joint morphology and function between vertical clingers and active arboreal quadrupeds. One approach to further testing these functional hypotheses is by analogy (Fleagle, 1976). The intraarticular labrum between the distal radius and scaphoid depression, weight-bearing midcarpal articulation, and dorsally wide capitate-trapezoid notch of lemuriform AAQs are also common in quadrupedal cebids, pitheciids, and cercopithecines (Yalden, 1972; Lewis, 1974, 1989; O'Connor, 1975; Jenkins, 1981; Fleagle and Meldrum, 1988). Like lemuriform AAQs, these quadrupedal New and Old World monkeys are also characterized by frequent antebrachiocarpal extension, midcarpal pronation, and compressive loading of the wrist joints during quadrupedal locomotion (Lewis, 1974, 1989). Interestingly *Hapalemur*, which is also known to frequently cling to vertical supports (Oxnard et al., 1990), most closely resembles quadrupedal lemuriforms in wrist morphology rather than VCs (Hamrick, in prep.).

Other extant primates possessing those carpal characters observed in Malagasy VCs are not so common, but those taxa that have them do clarify further the functional properties of such features. *Pithecia* (Fleagle and Meldrum, 1988) and *Galago senegalensis* (Hamrick, in prep.) also have a very curved midcarpal articulation, like the VCs studied here, which Fleagle and Meldrum (1988) related functionally to enhanced midcarpal supination during clinging postures. Jenkins (1981) showed that the hylobatid apes possess a palmarly wide and dorsally constricted trapezoid-capitate embrasure, much like the VCs examined in this study, related to increasing the range of midcarpal supination. Like lemuriform VCs, hylobatids also possess a powerful divergent pollex frequently used for grasping vertical supports (Van Horn, 1972; Susman et al., 1982). In-

deed Tuttle (1969), in considering the origin of the hylobatid hand, stated that "perhaps the prime selective biases were associated with capabilities for securely grasping vertical substrates of variable diameters." Finally, Fischer (1986) showed that hyraxes also supinate the wrist at the midcarpal joint during vertical clinging and climbing. These comparative examples indicate that midcarpal supination is critical for grasping vertical arboreal supports, and is often associated with a well-developed, divergent pollex.

Previous workers (Lewis, 1985; Sarmiento, 1987) have proposed that movements at the wrist during below-branch climbing and suspension, particularly axial rotation, also occur during climbing of vertical supports. Lewis (1985) underscored the 'overlapping character' of these two behaviors in hominoids, arguing that morphological adaptations for vertical climbing might be preadaptive for below-branch behaviors. The inferior radioulnar and ulnocarpal joints of indriids are clearly not specialized for the increased ranges of rotation and ulnar deviation found in the wrists of hominoids. Indriids lack significant expansion of the ulnar head and retain a prominent ulnar styloid process. Furthermore, VCs bear no major soft tissue modifications of the joint capsules which might expand their potential range of ulnar deviation and rotation at the ulnocarpal and inferior radioulnar joints. Evidence from lemuriform wrist morphology suggests that the use of vertical supports during postural behaviors does not require a tremendous range of wrist rotation. Hence, vertical climbing appears to require enhanced wrist joint mobility compared to vertical clinging. Frequent use of the forelimbs for orthograde postural behaviors therefore appears to require considerably less wrist joint rotation than frequent use of the forelimbs for orthograde locomotor behaviors (e.g. vertical climbing, slow climbing, brachiation).

Implications for interpreting fossil carpal remains

The identification of osseous carpal features functionally related to the movements associated with vertical clinging should also

shed light on the habitual postures of similarly sized fossil taxa. Napier's (Napier, 1967; Napier and Walker, 1967) characterization of the earliest primates as 'vertical clingers and leapers' can be tested against these additional lines of evidence. A complete functional analysis of early primate carpal remains is in progress (Hamrick, 1995, in prep.), but some preliminary analyses can be presented here. Some of the most enigmatic of these early primate postcranial remains are those of the adapiform primates *Smilodectes gracilis* and *Notharctus tenebrosus*. Covert (1985) observed several similarities between the postcranium of *Smilodectes* and extant VCs. Furthermore, Beard and Godinot (1988) and Godinot and Beard (1991) noted the carpus of *Smilodectes* had a more proximodistally directed triquetrohamate facet than its contemporary *Notharctus*. These contrasts led the authors to suggest more frequent vertical postures by *Smilodectes* and a greater commitment to quadrupedalism by *Notharctus*.

As noted earlier, lemuriform VCs differ from AAQs in several aspects of midcarpal joint morphology. Vertical clingers tend to have a tightly curved midcarpal joint, which allows a considerable range of ulnar deviation and supination. Quadrupedal lemuriforms have a flatter midcarpal surface, which is mechanically advantageous for supporting weight-bearing loads. This difference between AAQs and VCs in midcarpal curvature is due to the more proximally directed triquetrohamate facet of AAQs and more distally directed facet of VCs (Fig. 7). Bivariate plots of midcarpal curvature against midcarpal arc length demonstrate that both *Notharctus* and *Smilodectes* have very flat midcarpal joint surfaces compared to those of extant VCs (Fig. 13). In fact, curvature values for these two early primates fall at the very low end of the range observed for lemuriform AAQs (Fig. 13). Moreover, these results demonstrate that midcarpal curvature is quite similar between these two fossil primates, and that neither species shows a particularly strong resemblance to extant Malagasy VCs in midcarpal joint morphology. Future analyses (Hamrick, in prep.) will expand upon our understanding of carpal function in these early primates.

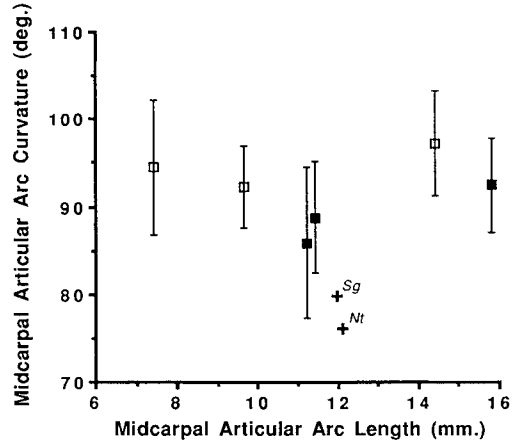


Fig. 13. Bivariate plots of midcarpal mediolateral curvature against midcarpal mediolateral arc length in vertical clingers (open squares), active arboreal quadrupeds (closed squares), and the notharctine primates *Smilodectes gracilis* (Sg; USNM 21815) and *Notharctus tenebrosus* (Nt; AMNH 11474). The squares represent species mean values and the thin vertical lines one standard deviation.

SUMMARY AND CONCLUSIONS

Two quite different patterns of carpal joint morphology are found in the Malagasy lemuriforms which are functionally related to contrasting postures of the hand and wrist during locomotor and postural behaviors. Lemuriform arboreal quadrupeds frequently extend the proximal wrist joint during quadrupedal weight-bearing positions (Fig. 8A), and these taxa possess an intracapsular fold between the dorsal scaphoid margin and the distal radius. The midcarpal surface of these AAQs is a weight-bearing one, where the triquetrum rests on a more proximally directed hamate surface and the proximal carpal row is pronated about the distal row (Fig. 8A). These taxa also have a mediolaterally expanded distal trapezoid surface, which reduces stress at the second carpometacarpal joint during the support phase of quadrupedal strides. The proximal joint of VCs is compacted and congruent during flexion (Fig. 8B), and these primates possess a thick dorsal radiocarpal ligament and deeply curved radiocarpal articulation. The midcarpal joint of VCs is impacted in a slightly supinated position (Fig. 8B), and differs from that of AAQs in having a dorsally

constricted capitate-trapezoid notch. VCs have a hypertrophied trapezium compared to the quadrupedal lemurs related to their divergent, powerful, grasping pollex.

The distribution of pronograde lemuri-form carpal characters among non-lemuri-form primate taxa indicates that arboreal quadrupedalism involving antebrachiocarpal extension and midcarpal pronation is a very common pattern of wrist joint movement in primates. The carpal characters associated with lemuri-form vertical clinging are far less common among primates. Certain similarities in carpal joint articular kinematics between hylobatids and indriids are quite interesting in light of their different locomotor behaviors. These similarities in carpal joint structure and function indicate that frequently grasping vertical arboreal substrates elicits major changes in the wrist articulations. These changes include structural adaptations for antebrachiocarpal flexion, midcarpal supination, and powerful pollical grasping. Results presented here also suggest that orthograde locomotor behaviors require a greater range of forearm rotation than do orthograde postural behaviors. The bony carpal features characteristic of extant VCs can be applied to infer potential movements of the wrist joints in fossil primate taxa.

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LITERATURE CITED

- Beard KC (1991) Vertical postures and climbing in the morphotype of Primatomorpha: Implications for locomotor evolution in primate history. In Y Coppens and B Senut (eds.): *Origine(s) de la Bipedie chez les Homi-nides*. Paris: CNRS, pp. 79–87.
- Beard KC, and Godinot M (1988) Carpal anatomy of *Smilodectes gracilis* (Adapiformes, Notharctinae) and its significance for lemuri-form phylogeny. *J. Hum. Evol.* 17:71–92.
- Bishop A (1964) Use of the hand in lower primates. In J Buettner-Janusch (ed.): *Evolutionary and Genetic Biology of Primates*. New York: Academic, pp. 133–225.
- Cartmill M (1974) Pads and claws in arboreal locomotion. In FA Jenkins Jr (ed.): *Primate Locomotion*. New York: Academic, pp. 45–83.
- Cartmill M (1985) Climbing. In M Hildebrand, D Bramble, K Liem, and D Wake (eds.): *Functional Vertebrate Morphology*. Cambridge, Mass.: Harvard University Press, pp. 73–88.
- Cartmill M, and Milton K (1974) The lorisiform wrist joint. *Am. J. Phys. Anthropol.* 41:471 (abstract).
- Cartmill M, and Milton K (1977) The lorisiform wrist joint and the evolution of "brachiating" adaptations in the Hominoidea. *Am. J. Phys. Anthropol.* 47:249–272.
- Corruccini RS (1977) Features of the prosimian wrist joint in relation to hominoid specializations. *Acta Anat.* 99:440–444.
- Corruccini RS, Ciochon RL, and McHenry HM (1975) Osteometric shape relationships in the wrist joint of some anthropoids. *Folia Primatol.* 24:250–274.
- Covert HH (1985) The skeleton of *Smilodectes gracilis*. *Am. J. Phys. Anthropol.* 66:159 (abstract).
- Dagosto MD (1994) Testing positional behavior of Malagasy lemurs: a randomization approach. *Am. J. Phys. Anthropol.* 94:189–202.

- Darroch JN, and Mosimann JE (1985) Canonical and principal components of shape. *Biometrika* 72: 241–252.
- Demes B, and Jungers WL (1993) Long bone cross-sectional dimensions, locomotor adaptations and body size in prosimian primates. *J. Hum. Evol.* 25:57–74.
- Etter H-UF (1978) Lorisiform hands and their phylogenetic implications: A preliminary report. In DJ Chivers and KA Joysey (eds.): *Recent Advances in Primatology*, Vol. III. Evolution. London: Academic, pp. 161–170.
- Fischer MA (1986) Die Stellung der Schliefer (Hyracoidea) im phylogenetischen System der Eutheria. *Cour. Forsch.-Inst. Senckenberg* 84:1–132.
- Fleagle JG (1976) Locomotion and posture of the Malayan siamang and implications for hominoid evolution. *Folia Primatol.* 26:245–269.
- Fleagle JG (1977) Locomotor behavior and skeletal morphology of sympatric Malaysian leaf monkeys (*Presbytis obscura* and *Presbytis melalophos*). *Yrbk. Phys. Anthropol.* 20:440–453.
- Fleagle JG (1988) *Primate Adaptation and Evolution*. New York: Academic Press.
- Fleagle JG, Stern JT Jr, Jungers WL, Susman R, Vangor AK, and Wells JP (1981) Climbing: A biomechanical link with brachiation and with bipedalism. *Symp. Zool. Soc. Lond.* 48:359–375.
- Fleagle JG, and Meldrum DJ (1988) Locomotor behavior and skeletal morphology of two sympatric pitheciine monkeys, *Pithecia pithecia* and *Chiropotes satanas*. *Am. J. Primatol.* 16:227–249.
- Gebo DL (1985) The nature of the primate grasping foot. *Am. J. Phys. Anthropol.* 67:269–277.
- Gebo DL (1987) Locomotor diversity in prosimian primates. *Am. J. Primatol.* 13:271–281.
- Gebo DL, and Dagosto M (1988) Foot anatomy, climbing, and the origin of the Indriidae. *J. Hum. Evol.* 17:135–154.
- Godinot M, and Beard KC (1991) Fossil primate hands: A review and an evolutionary inquiry emphasizing early forms. *Hum. Evol.* 6:307–354.
- Groves CP, and Eaglen RH (1988) Systematics of the Lemuridae (Primates, Strepsirhini). *J. Hum. Evol.* 17:513–538.
- Hamrick MW (1995) Wrist morphology and positional behavior of adapiform primates. *Am. J. Phys. Anthropol.* [Suppl.] 20:104–105 (abstract).
- Harvey PH, and Pagel MD (1991) *The Comparative Method in Evolutionary Biology*. Oxford: Oxford University Press.
- Hildebrand M (1985) Walking and running. In M Hildebrand, D Bramble, K Liem, and D Wake (eds.): *Functional Vertebrate Morphology*. Cambridge, Mass.: Harvard University Press, pp. 89–109.
- Hughes H (1944) The evolution and functional significance of the transverse carpal arch of man. *J. Anat.* 78:167–172.
- Jenkins FA Jr (1981) Wrist rotation in primates: A critical adaptation for brachiators. *Symp. Zool. Soc. Lond.* 48:429–451.
- Jenkins FA Jr, and Fleagle JG (1975) Knuckle-walking and the functional anatomy of the wrist in living apes. In RH Tuttle (ed.): *Primate Functional Morphology and Evolution*. The Hague: Mouton, pp. 213–227.
- Jolly A (1966) *Lemur Behavior*. Chicago: University of Chicago Press.
- Jouffroy FK (1975) Osteology and myology of the lemuriform postcranial skeleton. In I Tattersall and RW Sussman (eds.): *Lemur Biology*. New York: Plenum, pp. 149–192.
- Latimer B, and Lovejoy O (1989) The calcaneus of *Australopithecus afarensis* and its implications for the evolution of bipedality. *Am. J. Phys. Anthropol.* 78:369–386.
- Lewis OJ (1965) Evolutionary change in the primate wrist and inferior radioulnar joints. *Anat. Rec.* 151:275–286.
- Lewis OJ (1969) The hominoid wrist joint. *Am. J. Phys. Anthropol.* 30:251–268.
- Lewis OJ (1971) Brachiation and the early evolution of the Hominoidea. *Nature* 230:577–578.
- Lewis OJ (1972) Osteological features characterizing the wrists of monkeys and apes, with a reconsideration of this region in *Dryopithecus (Proconsul) africanus*. *Am. J. Phys. Anthropol.* 36:45–58.
- Lewis OJ (1974) The wrist articulations of the Anthropoidea. In FA Jenkins Jr (ed.): *Primate Locomotion*. New York: Academic, pp. 143–169.
- Lewis OJ (1985) Derived morphology of the wrist articulations and theories of hominoid evolution. Part I. The lorisine joints. *J. Anat.* 140:447–460.
- Lewis OJ (1989) *Functional Morphology of the Evolving Hand and Foot*. Oxford: Clarendon Press.
- MacConaill (1973) A structuro-functional classification of synovial articular units. *Irish J. Med. Sci.* 142:19–26.
- MacLarnon AM (1989) Applications of the reflux instruments in quantitative morphology. *Folia Primatol.* 53:33–49.
- Martin RD (1990) *Primate Origins and Evolution*. New Jersey: Princeton University Press.
- Meldrum DJ (1991) Kinematics of the cercopithecine foot on arboreal and terrestrial substrates with implications for the interpretation of hominid terrestrial adaptations. *Am. J. Phys. Anthropol.* 84:273–289.
- Mendel FC (1979) The wrist joint of two-toed sloths and its relevance to brachiating adaptations in the Hominoidea. *J. Morphol.* 162:413–424.
- Mosimann JE, and James FC (1979) New statistical methods for allometry with application to Florida red-winged blackbirds. *Evolution* 33:444–459.
- Napier JR (1967) Evolutionary aspects of primate locomotion. *Am. J. Phys. Anthropol.* 27:333–342.
- Napier JR, and Walker AC (1967) Vertical clinging and leaping—a newly recognized category of locomotor behaviour in primates. *Folia Primatol.* 6:204–219.
- Neff NA, and Marcus LF (1980) *A Survey of Multivariate Methods for Systematics*. New York: American Museum of Natural History.
- Nieschalk U, and Demes B (1993) Biomechanical determinants of reduction of the second ray in Lorissinae. In H Preuschoft and D Chivers (eds.): *Hands of Primates*. New York: Springer-Verlag.
- O'Connor BL (1975) The functional morphology of the cercopithecoid wrist and inferior radioulnar joints, and their bearing on some problems in the evolution of the Hominoidea. *Am. J. Phys. Anthropol.* 43:113–122.
- O'Connor BL, and Rarey KE (1979) Normal amplitudes

- of radioulnar pronation and supination in several genera of anthropoid primates. *Am. J. Phys. Anthropol.* 51:39–44.
- Oxnard CE, Crompton RH, and Lieberman SS (1990) *Animal Lifestyles and Anatomies: The Case of the Prosimian Primates*. Seattle: University of Washington Press.
- Rayner JMV (1985) Linear relations in biomechanics: The statistics of scaling functions. *J. Zool.* 206: 415–439.
- Sarmiento EE (1987) The phylogenetic position of *Oreopithecus* and its significance in the origin of the Hominoidea. *Am. Mus. Novitates* 2881:1–44.
- Sarmiento EE (1988) Anatomy of the hominoid wrist joint: Its evolutionary and functional implications. *Int. J. Primatol.* 9:281–345.
- Schmitt D (1993) Transverse substrate reaction forces on the forelimb during arboreal and terrestrial quadrupedalism in monkeys. *Am. J. Phys. Anthropol.* [Suppl.] 16:174.
- Simons EL (1972) *Primate Evolution*. New York: Macmillan.
- Simons EL, and Rumpler Y (1988) *Eulemur*: New generic name for species of *Lemur* other than *Lemur catta*. *C. R. Acad. Sci. Paris* 307:547–551.
- Sokal R, and Rohlf F (1981) *Biometry*. New York: W.H. Freeman.
- Susman RL, Jungers WL, and Stern JT Jr (1982) The functional morphology of the accessory interosseous muscle in the gibbon hand: determination of locomotor and manipulatory compromises. *J. Anat.* 134:111–120.
- Susman RL, Stern JT Jr, and Jungers WL (1984) Arboreality and bipedality in the Hadar hominids. *Folia Primatol.* 43:113–156.
- Tattersall I (1982) *The Primates of Madagascar*. New York: Columbia University Press.
- Tattersall I, and Schwartz J (1991) Phylogeny and nomenclature in the *Lemur*-group of Malagasy strepsirrhine primates. *Anthropol. Papers of the Am. Mus. of Nat. Hist.* 69:1–18.
- Tuttle RH (1967) Knuckle-walking and the evolution of hominoid hands. *Am. J. Phys. Anthropol.* 26:171–206.
- Tuttle RH (1969) Quantitative and functional studies on the hands of Anthroipoidea. *J. Morphol.* 128:309–364.
- Van Horn RN (1972) Structural adaptations to climbing in the gibbon hand. *Am. Anthropol.* 74:326–333.
- Walker A (1974) Locomotor adaptations in past and present prosimian primates. In FA Jenkins Jr (ed.): *Primate Locomotion*. New York: Academic, pp. 349–381.
- Walker A (1979) Prosimian locomotor behavior. In GA Doyle and RD Martin (eds.): *The Study of Prosimian Behavior*. New York: Academic, pp. 543–565.
- Ward SC, and Sussman RW (1979) Correlates between locomotor anatomy and behavior in two sympatric species of *Lemur*. *Am. J. Phys. Anthropol.* 50:575–590.
- Whitehead P (1993) Aspects of the anthropoid wrist and hand. In D Gebo (ed.): *Postcranial Adaptation in Non-human Primates*. DeKalb: Northern Illinois University Press, pp. 96–120.
- Yalden DW (1972) The form and function of the carpal bones in some arboreally adapted mammals. *Acta Anat.* 82:383–406.
- Yoder A (1994) Molecular systematics of the Lemuridae: is *Eulemur* necessary? *Am. J. Phys. Anthropol.* [Suppl.] 18:213–213 (abstract).
- Zar JH (1984) *Biostatistical Analysis*. Englewood Cliffs: Prentice-Hall.